

INTER-SPECIFIC ASSOCIATIONS INVOLVING SPIDERS: KLEPTOPARASITISM, MIMICRY AND MUTUALISM

MARK A. ELGAR

Elgar, M.A. 1993 11 11: Inter-specific associations involving spiders: kleptoparasitism, mimicry and mutualism. *Memoirs of the Queensland Museum* 33(2): 411-430. Brisbane. ISSN 0079-8835.

Many spiders have life-styles that involve a relatively close and prolonged association with another species; for example, between a specialist predator and its prey species, or a species may rely on another for either protection from predators or providing a suitable place to live. In asymmetric relationships, where individuals of one species benefit at the expense of the other, each species may act as a selection pressure on the other species. This can result in the evolution of specific adaptations and counter-adaptations that are evident in at least three kinds of inter-specific associations between spiders. These associations, namely kleptoparasitism, mimicry and mutualism are reviewed here. Our understanding of the evolution of these fascinating systems remains limited, despite numerous anecdotal accounts, because only a few studies are experimental. The purpose of this review is two-fold: to illustrate the use of comparative and experimental studies for understanding the evolutionary significance of these inter-specific relationships, and to highlight those gaps in our knowledge that might benefit from this approach. □ *Inter-specific associations, spiders, kleptoparasitism, mimicry, mutualism.*

Mark A. Elgar, Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia; 18 January, 1993.

Individuals of one species can affect individuals of another as a result of competition, predation, parasitism or mutualism. The evolutionary implications of any association between two or more species depends critically on the frequency and nature of the interaction. For example, a species may be the prey of many species of generalist predators. While these predators may represent an important selective pressure favouring anti-predator responses in the prey species, the adaptations of the prey may have little impact on the reproductive success of the predators. In contrast, a predator that preys on only one species can be an important selective force favouring anti-predator adaptations in that species. In turn, the prey species anti-predator adaptations can exert a selective pressure on the predator, favouring improved predatory abilities. Thus, each species acts as a selection pressure on the other, favouring adaptations and counter-adaptations, perhaps leading to characteristics that are increasingly specific to the relationship. However, these improvements need not necessarily change the relative position of each protagonist (Dawkins and Krebs, 1979). The evolution of these specific adaptations and counter-adaptations depends on both the frequency of the interactions and the effects of each protagonist. Host-parasite systems provide a rich seam of examples of such evolutionary processes

(e.g. Endler, 1986; Davies *et al.*, 1989; Toft *et al.*, 1991), but there is also some evidence for similar processes in predator-prey systems (e.g. Brodie and Brodie, 1991; Endler, 1991).

INTER-SPECIFIC ASSOCIATIONS IN SPIDERS

Research on the behaviour and ecology of spiders has, with a few notable exceptions, focussed on issues involving single species (e.g. Humphreys, 1988), including foraging behaviour (Reichert and Luczak, 1982; Vollrath, 1987a; Uetz, 1992), habitat choice (e.g. Reichert and Gillespie, 1986), intraspecific competition (e.g. Reichert, 1982), courtship and mating (e.g. Robinson and Robinson, 1982; Elgar, 1992) and social behaviour (Buskirk, 1981; Elgar and Godfray, 1987; Uetz, 1988). Nevertheless, some spiders have relatively specific and prolonged relationships with other species. These relationships often involve predation or avoiding predation, and perhaps a reason why inter-specific interactions involving spiders have been neglected is that spiders are frequently perceived as generalist predators; cursorial or wandering spiders attack any vulnerable prey that they can find, while web-building spiders simply capture any prey that is caught in their web. However, the view that spiders are generalist predators is mis-

leading. Many spiders prey on only a few species using foraging techniques that include building specialised webs; producing chemical compounds that attract prey; utilising the webs or capturing capabilities of other spiders; mimicking prey behaviour; and cooperative foraging (see reviews in Stowe, 1986; Nentwig, 1987). Clearly, the survival and reproductive success of both predator and prey will depend on their predatory and defensive behaviours, and the degree to which the predator depends on the prey as a source of food. Not all associations between spiders and other invertebrates are predator-prey relationships; some species depend on other species for protection from predators, or providing suitable places to live. This review will focus on three inter-specific relationships involving spiders: kleptoparasitism, mimicry and mutualism.

A detailed understanding of the nature of these inter-specific associations will benefit from both experimental and comparative studies. The former can provide insight into both the fitness effects of the association on individuals of each species, and the importance of particular species' traits for maintaining the association. Comparative studies can provide further insight into the selection pressures responsible for the evolution of the association; reveal the implications of these associations for other aspects of the species life-history characteristics; and help formulate ideas that can be subsequently examined experimentally (see Harvey and Pagel, 1992 for review). While emphasising the evolutionary dynamic nature of inter-specific associations, a central theme of this review is to illustrate the use of comparative and experimental studies for understanding these systems, and also to highlight those gaps in our knowledge of arachnid inter-specific associations that might benefit from this evolutionary approach.

KLEPTOPARASITIC ASSOCIATIONS

The webs of spiders are host to numerous insects, including flies, damselflies and wasps (see reviews in Vollrath, 1984, 1987b; Nentwig and Heimer, 1987). Most descriptions of these guests are anecdotal, and consequently the nature of the relationship is poorly understood. The webs of many spiders are also host to numerous other spiders that obtain food from prey caught in the host's web. These spider guests, commonly referred to as kleptoparasites, are represented in at least four families, including the Dictynidae,

Mysmenidae, Symphytognathidae and Theridiidae (Table 1). Of these spiders, the genus *Argyrodes* (Theridiidae) is the best documented (see Vollrath, 1984, 1987b).

EVIDENCE OF KLEPTOPARASITISM

Argyrodes were originally described as commensals: *Argyrodes* benefit by feeding on the prey items that are caught in the host's web, but the host is not disadvantaged because these prey items do not form part of its diet (e.g. Belt, 1874). However, subsequent behavioural and ecological studies revealed that individual *Argyrodes* remove prey that might otherwise be consumed by the predator. These observations suggest that the relationship between *Argyrodes* and their hosts is more accurately described as kleptoparasitic rather than commensal (see Vollrath, 1984, 1987b).

In fact, kleptoparasitism may also be an inappropriate description. A kleptoparasitic relationship implies that one partner in the symbiosis benefits at the expense of the other, and that the kleptoparasite has certain characteristics that are adaptations to this lifestyle. Studies of several species associations leave little doubt that the latter contention is correct. For example, the symphytognathid *Curimagua bayano* inhabits the webs of a large mygalomorph *Diplura*, either climbing about the funnel web or remaining on the host (Vollrath, 1978). After a *Diplura* has caught, masticated and enveloped a prey item in digestive fluids, the kleptoparasite descends to the prey item and imbibes the liquidized prey. Interestingly, the anatomy of the mouth of *C. bayano* apparently prevents it from being able to capture, hold or masticate its own prey, suggesting that it is an obligate kleptoparasite (Vollrath, 1978).

Several behaviours of *Argyrodes* appear to be adaptations that are specifically related to their kleptoparasitic lifestyle. These spiders can move throughout the web, apparently undetected by the host, and the attempts of the kleptoparasites to obtain prey items may vary according to the behaviour of the host (Vollrath, 1984, 1987b). There are several mechanisms by which kleptoparasitic *Argyrodes* avoid detection or capture by the host: many species drop from the web when challenged by the host, *A. antipodianus* swings away from the web when the host is agitated (Whitehouse, 1986), and *A. ululans* cuts holes in the tangle web of its social spider host *Anelosimus eximius*, forming a tunnel that apparently facilitates escape (Cangialosi, 1991).

Surprisingly, the evidence that the presence of *Argyrodes* has a negative effect on the reproductive success of the host has not been directly assessed. For example, there are no experimental evidence that the growth rate or fecundity of the host is reduced by the presence of *Argyrodes* (or any other genera of kleptoparasites). Instead, the negative impact of *Argyrodes* on its host has been inferred primarily from either the behaviour of the host (e.g. Larcher and Wise, 1985), or from estimates of the energetic costs derived from the loss of prey items obtained by *Argyrodes*. For example, the number of prey items consumed by *Nephila clavipes* is reduced with increasing numbers of *Argyrodes* on the web (Rypstra, 1981), and *A. ululans* removes around 26% of the prey items that are caught in the web of its host *Anelosimus eximius* (Cangialosi, 1990b). Vollrath (1981) examined the potential costs of *Argyrodes* by estimating the energetic requirements of a single kleptoparasite. The daily energy requirements of the 3-4 mg *A. elevatus* is 0.82 J, about 0.5% of the daily requirements of its 975mg (*Nephila clavipes*) host. This proportion increases with larger numbers of kleptoparasites per web; over 40 individuals have been counted on a single *Nephila* web (although the average is 2.2 kleptoparasites per web), suggesting a potentially high energetic cost of this relationship (Vollrath, 1981).

If kleptoparasites exact a cost on host reproductive success, then selection should favour any trait that enables the hosts to reduce that cost. There are several mechanisms by which hosts might reduce the cost of kleptoparasitism: recovering the prey from the kleptoparasite; reducing the kleptoparasites access to the prey; or simply abandoning the web and building another elsewhere. Interestingly, hosts appear to be inefficient at recovering prey (Vollrath, 1979a, b; Rypstra, 1981) although several host species reduce access to their prey by chasing the kleptoparasites (Cangialosi, 1990b) or concealing the prey in retreats (see Cangialosi, 1990b). Larcher and Wise (1985) demonstrated experimentally that hosts are more likely to abandon webs when *Argyrodes* are present than absent. *Nephila clavipes* relocates its web when it is infested with large numbers of kleptoparasites (Rypstra, 1981), although the behaviour of *N. clavipes* may be a response to lower feeding rates, rather than to numbers of kleptoparasites.

Social or communal spiders appear to have fewer defensive options against high kleptoparasite loads, and this cost may be higher if the

number of kleptoparasites per web is greater in larger colonies. For example, *Nephila edulis* builds webs in aggregations, and webs in aggregations have higher kleptoparasite loads and infestation rates than those found alone (Elgar, 1989). Re-locating a web away from an aggregation may reduce kleptoparasite load, but the host subsequently does not benefit from the foraging and predator defense advantages of living within an aggregation (e.g. see Uetz, 1988). Moving web sites to reduce kleptoparasite load may not be possible for some social spiders, such as *Anelosimus* that build substantial, permanent webs. Indeed, high kleptoparasite loads are apparently responsible for the demise of some *Anelosimus* colonies (Cangialosi, 1990b) but not others (Vollrath, 1982).

Like their hosts, individual kleptoparasites may also react to variation in prey capture rates. The feeding rates of kleptoparasites are likely to be influenced by both the prey capture rate of the host and the number of other kleptoparasites on the web. Host web capture rates may vary according to both the location and the size of the web. The number of kleptoparasites increases with the web size of several host species (e.g. Elgar, 1989; Cangialosi, 1990a), possibly because larger webs have higher web capture rates that can support more kleptoparasites. Web-building spiders relocate their webs according to prey capture rates (e.g. Gillespie and Caraco, 1987), and *Argyrodes* may behave similarly by moving to different webs (but see Larcher and Wise, 1985). It would be interesting to establish experimentally whether the emigration rate of individual *Argyrodes* increases as a result of lower web capture rates or increased numbers of conspecifics. If the latter, it is possible that the distribution of *Argyrodes* within a population of hosts, particularly those hosts that aggregate, could be predicted by the ideal free distribution (see Milinski and Parker, 1991).

A possible option for kleptoparasites that experience a low feeding rate is to capture and consume the host before moving to the web of another host (e.g. Tanaka, 1984). Some species of *Argyrodes* are either obligate or facultative predators of their hosts (see Table 1). Predatory *Argyrodes* can capture the host through mimicking a prey item (e.g. Whitehouse, 1986) or simply advancing toward the host and attacking it. Such a specialised form of predation is not uncommon in spiders, and has been recorded in several families (e.g. Jackson, 1987; Jackson and Blest, 1982; Jackson and Brassington, 1987; Jarman

TABLE 1: Spiders that are presumed to be kleptoparasites of web-building spiders. Families: Ag, Agelenidae; Am, Amaurobiidae; Ap, Aphantochilidae; Ar, Araneidae; Cl, Clubionidae; Co, Corinnidae; De, Deinopidae; Di, Dipluridae; Er, Eresidae; Gn, Gnaphosidae; Lin, Linyphiidae; Lio, Liocranidae; Ph, Pholcidae; Pro, Prodidomidae; Sa, Salticidae; Td, Theridiidae; Tm, Thomisidae; Ul, Uloboridae; Zo, Zodariidae. Agg, Aggregates; Soc, Social; Sol, Solitary. Web types: O, orb; T, tangle; S, sheet; F, funnel; Sp, space. Body sizes in mm.

Kleptoparasitic taxa	Body size		Host					Guests per web	Assoc*	Source
	♂	♀	Family	Species	Size	Web	Social			
Dictynidae										
<i>Archaedictyna ulova</i>			Er	<i>Stegadyphus</i>		T	Soc		K	Griswold & Meikle-Griswold (1987)
Heteropodidae										
<i>Olios diana</i>			Am	<i>Badumna candida</i>		T	Soc	20	K	Jackson (1987)
<i>O. sp. indet.</i>			Am	<i>Badumna candida</i>		T	Soc	10	K	Jackson (1987)
<i>O. lamarchi</i>			Er	<i>Stegodyphus sarasinorum</i>		T	Soc	10	K	Jackson (1987)
<i>O. obesulus</i>			Er	<i>Stegodyphus sarasinorum</i>		T	Soc	8	K	Jackson (1987)
Mysmenidae										
<i>Isela okuncana</i>			Di	<i>Allothelpe terretis</i>		F	Sol		K	Griswold (1985)
<i>Kilifuz inquilina</i>			Di	<i>Thelechoris karschi</i>		F			K	Coyle <i>et al.</i> (1991)
<i>Mysmenopsis archeri</i>			Ph			T			K	Baptisa (1988)
<i>M. capue</i>			Ar	<i>Cyrtophora</i>		O			K	Baert (1990)
<i>M. cidreliala</i>			Di						K	Coyle <i>et al.</i> (1991)
<i>M. cienga</i>			Ar	<i>Cyrtophora</i>		O			K	Baert (1990)
<i>M. dipluroamiga</i>			Di	<i>Diplura</i>		S			K	Vollrath (1978)
<i>M. furtiva</i>	1.5		Di	<i>Ischnothele xera</i>		T	Sol	14	K	Coyle <i>et al.</i> (1991)
<i>M. gambia</i>			Di	<i>Diplura</i>		S			K	Vollrath (1978)
<i>M. hauscar</i>			Di						K	Coyle <i>et al.</i> (1991)
<i>M. ischnanigo</i>			Di	<i>Diplura</i>		S			K	Vollrath (1978)
<i>M. monticala</i>			Di	<i>Ischnothele sp.</i>		T	Sol	4	K	Coyle & Meigs (1989)
<i>M. pochucutec</i>			Di						K	Coyle <i>et al.</i> (1991)
<i>M. palpalis</i>			Di						K	Coyle <i>et al.</i> (1991)
<i>M. tibialis</i>			Di						K	Coyle <i>et al.</i> (1991)
<i>M. sp. indet.</i>			Di	<i>Ischnothele reggae</i>					K	Coyle <i>et al.</i> (1991)
Oonopidae										
<i>Oonops pulcher</i>	2.0	1.5	Am	<i>Amaurobins fenestralis</i>	8	T			K	Bristowe (1958)
Salticidae										
<i>Simaetha puetula</i>	7.0	7.0	Am	<i>Badumna candida</i>		T	Soc		KP	Jackson (1985)
Symphytognathidae										
<i>Curimagna bayano</i>	1.3	1.3	Di	<i>Diplura sp.</i>	40	S	Sol		K	Vollrath (1978)
Theridiidae										
<i>Argyrodes antipodians</i>			Ag	<i>Cambridgea sp.</i>		F	Sol		KP	Whitehouse (1988a)
<i>A. antipodians</i>			Ag	<i>Stiphidion</i>		F	Sol		KP	Whitehouse (1988a)
<i>A. antipodians</i>			Am	<i>Badumna longinquus</i>		Sp	Sol		KP	Whitehouse (1988a)
<i>A. antipodians</i>			Ar	<i>Araneus crassa</i>		O	Sol		KP	Whitehouse (1988a)
<i>A. antipodians</i>			Ar	<i>Eriophora pustulosa</i>	13	O	Sol		KP	Whitehouse (1988a)
<i>A. antipodians</i>			Ar	<i>Cyclosa trilobata</i>	8	O	Sol		KP	Whitehouse (1988a)
<i>A. antipodians</i>			Ar	<i>Leucange dromedaria</i>		O	Sol		KP	Whitehouse (1988a)
<i>A. antipodians</i>			Ph	<i>Pholcus phalangoides</i>		Sp	Sol		KP	Whitehouse (1988a)
<i>A. antipodians</i>			Td	<i>Achaearanea</i>		T	Sol		KP	Whitehouse (1988a)
<i>A. antipodians</i>	3.0	2.5	Ar	<i>Cyrtophora hirta</i>	14	O	Sol		K	Elgar <i>et al.</i> (1983)
<i>A. antipodians</i>	3.0	2.5	Ar	<i>Nephila edulis</i>	21	O	Agg		K	Elgar (1989)

Kleptoparasitic taxa	Body size		Host				Guests per web	Assoc*	Source	
	♂	♀	Family	Species	Size	Web				Social
<i>A. argyroides</i>			Ar	<i>Cyrtophora citricola</i>		O			K	Vollrath (1984)
<i>A. atopus</i>	2.4	3.4	Ar	<i>Nephila clavipes</i>	25	O	Agg	5	K	Vollrath (1987)
<i>A. attenuatus</i>	17.0	9.3	none							Eberhard (1979a)
<i>A. baboquinari</i>	3.7	3.5	Td	<i>Latrodectus</i>		T	Sol		K	Exline & Levi (1962)
<i>A. babaquivari</i>	3.7	3.5	Ul	<i>Philapanella aweni</i>	6	O	Agg		KP	Smith Trail (1980)
<i>A. cancellatus</i>	3.2	3.8	Ag	<i>Agelenopsis</i>		F			K	Exline & Levi (1962)
<i>A. cancellatus</i>	3.2	3.8	Ar	<i>Argiope aurantia</i>	22	O			K	Exline & Levi (1962)
<i>A. cancellatus</i>	3.2	3.8	Ar	<i>Araneus strix</i>		O			K	Exline & Levi (1962)
<i>A. cancellatus</i>	3.2	3.8	Ar	<i>Mecynogea lemniscata</i>		O			K	Exline & Levi (1962)
<i>A. cancellatus</i>	3.2	3.8	Ar	<i>Metepeira labyrinthea</i>		O	Sol		K	Exline & Levi (1962)
<i>A. cancellatus</i>	3.2	3.8	Ar	<i>Nephila clavipes</i>	25	O	Agg		K	Exline & Levi (1962)
<i>A. cancellatus</i>	3.2	3.8	Ar	<i>Verrucosa arenta</i>	9	O			K	Exline & Levi (1962)
<i>A. cancellatus</i>	3.2	3.8	Li	<i>Frontinella pyramitela</i>	4	S			K	Exline & Levi (1962)
<i>A. cancellatus</i>	3.2	3.8	Ph	<i>Pholcus</i>		space	Sol		K	Exline & Levi (1962)
<i>A. cancellatus</i>	3.2	3.8	Td	<i>Theridion tepidariorum</i>	7	T			K	Exline & Levi (1962)
<i>A. caudatus</i>	3.1	3.9	Ar	<i>Argiope argentata</i>	16	O	Sol		K	Smith Trail (1980)
<i>A. cochleafarma</i>	2.7	3.7	Ar	<i>Argiope</i>		O			K	Exline & Levi (1962)
<i>A. cachleaforma</i>	2.7	3.7	Ar	<i>Gasteracantha</i>		O			K	Exline & Levi (1962)
<i>A. calubrinus</i>	25.0		none							Eberhard (1986)
<i>A. cardillera</i>	3.6	3.1	Ar	<i>Gasteracantha</i>		O			K	Exline & Levi (1962)
<i>A. cylindricus</i>			Ar	<i>Araneus ventricus</i>		O	Sol		K	Shinkai (1988)
<i>A. dracus</i>	2.3	2.6	Ar	<i>Nephila clavipes</i>	25	O	Agg	5	K	Vollrath (1987)
<i>A. elevatus</i>	3.4	4.0	Ar	<i>Argiope argentata</i>	16	O		4	K	Vollrath (1979)
<i>A. elevatus</i>	3.4	4.0	Ar	<i>Gasteracantha</i>		O			K	Exline & Levi (1962)
<i>A. elevatus</i>	3.4	4.0	Ar	<i>Nephila clavipes</i>	25	O	Agg	5	K	Vollrath (1979)
<i>A. fictilium</i>	10.0	5.0	Ar	<i>Araneus</i>		O			KP	Exline & Levi (1962)
<i>A. fictilium</i>	10.0	5.0	Li	<i>Frontinella communis</i>	4	S	Agg		KP	Wise (1982)
<i>A. fictilium</i>	10.0	5.0	Ul	<i>Philapanella oweni</i>	6	O	Agg		KP	Smith Trail (1980)
<i>A. fictilium</i>	10.0	5.0	none							Exline & Levi (1962)
<i>A. fissifrons</i>	7.0		Ag	<i>Agelena limbata</i>	16	F	Agg	2	KP	Tanaka (1984)
<i>A. fissifrons</i>	7.0		Lin	<i>Linyphia</i>		S			KP	Tanaka (1984)
<i>A. fissifrons</i>	7.0		Td	<i>Theridion japonicum</i>		T			KP	Tanaka (1984)
<i>A. fissifrons</i>	7.0		Ul	<i>Philapanella sp.</i>	3	O	Agg	3	KP	Elgar (pers obs)
<i>A. fissifrons</i>	7.0		Ul	<i>Uloborus varians</i>		O			KP	Tanaka (1984)
<i>A. flagellum</i>			none							Eberhard (1986)
<i>A. globasus</i>	2.3	2.3	Ar	<i>Nephila clavipes</i>	25	O	Agg		K	Exline & Levi (1962)
<i>A. incisifrons</i>			Ar	<i>Cyrtaphara hirta</i>	14	O	Sol		K	Elgar <i>et al.</i> (1983)

Table 1. continued

Table 1. *continued*

Kleptoparasitic taxa	Body size		Host					Guests per web	Assoc*	Source
	♂	♀	Family	Species	Size	Web	Social			
<i>A. incurtus</i>	3.8	2.2	Td	<i>Achaearanea mundulo</i>	6	T	Sol	5	KP	Gray & Anderson (1989)
<i>A. longissimus</i>	24.0	19.0	none							Exline & Levi (1962)
<i>A. miniaceus</i>			Ar	<i>Nephila maculoto</i>	43	O			K	Robinson & Robinson (1973)
<i>A. nephilae</i>	1.7	2.2	Ar	<i>Argiope</i>		O			K	Exline & Levi (1962)
<i>A. nephilae</i>	1.7	2.2	Ar	<i>Cyrtophora moluccensis</i>	19	O	Agg		K	Berry (1987)
<i>A. nephilae</i>	1.7	2.2	Ar	<i>Gasteracantha</i>		O			K	Exline & Levi (1962)
<i>A. nephilae</i>	1.7	2.2	Ar	<i>Neoscona</i>		O			K	Exline & Levi (1962)
<i>A. nephiloe</i>	1.7	2.2	Ar	<i>Nephila</i>		O			K	Exline & Levi (1962)
<i>A. nephiloe</i>	1.7	2.2	Ar	<i>Nephila maculata</i>	43	O			K	Robinson & Robinson (1973)
<i>A. pluto</i>	3.9	3.7	Ar	<i>Argiope ourontio</i>	22	O			K	Exline & Levi (1962)
<i>A. pluto</i>	3.9	3.7	Ar	<i>Metepeiro lobyrinthea</i>		O	Sol		K	Exline & Levi (1962)
<i>A. pluto</i>	3.9	3.7	Td	<i>Latrodectus</i>		T	Sol		K	Exline & Levi (1962)
<i>A. proboscifo</i>	2.6	2.9	Ar	<i>Gasteracantho</i>		O			K	Exline & Levi (1962)
<i>A. projiciens</i>	4.0	3.2	Ar	<i>Metazygia</i> sp.		O	Sol		KP	Eberhard (1986)
<i>A. sp. A</i>			Ar	<i>Nephila clavipes</i>	25	O	Agg	2	K	Rypstra (1981)
<i>A. sp. B</i>			Ar	<i>Cyrtophora moluccensis</i>	19	O	Agg		KP	Lubin (1974)
<i>A. sp. C</i>			Ar	<i>Gasteracantho</i>		O		23		Vollrath (1981)
<i>A. subdolos</i>	2.6	2.8	Ul	<i>Philoponella oweni</i>	6	O	Agg		K	Smith Trail (1980)
<i>A. trigonum</i>	4.2	2.5	Ag	<i>Agelena limbata</i>	16	F	Agg		KP	Suter <i>et al.</i> (1989)
<i>A. trigonum</i>	4.2	2.5	Ag	<i>Agelenopsis</i>		F				Exline & Levi (1962)
<i>A. trigonum</i>	4.2	2.5	Ar	<i>Mecynogeo lenniscato</i>		O			KP	Wise (1982)
<i>A. trigonum</i>	4.2	2.5	Ar	<i>Metepira lobyrintheo</i>		O	Sol		KP	Larcher & Wise (1985)
<i>A. trigonum</i>	4.2	2.5	Lin	<i>Linyphia marginata</i>	5	S			KP	Exline & Levi (1962)
<i>A. trigonum</i>	4.2	2.5	Lin	<i>Neriere radiota</i>	5	S	Sol		KP	Larcher & Wise (1985)
<i>A. trigonum</i>	4.2	2.5	Td	<i>Latrodectus</i>		T	Sol			Exline & Levi (1962)
<i>A. trigonum</i>	4.2	2.5	Td	<i>Theridion zelotypum</i>	4	T			KP	Exline & Levi (1962)
<i>A. trigonum</i>	4.2	2.5	Lin	<i>Frontinella pyramitela</i>	4	S			KP	Suter <i>et al.</i> (1989)
<i>A. ululons</i>	4.0	3.7	Ar	<i>Nephilo clavipes</i>	25	O	Agg		K	Exline & Levi (1962)
<i>A. ululans</i>	4.0	3.7	Td	<i>Anelosimus eximius</i>		T	Soc		K	Cangialosi (1990a)
<i>A. weyrauchi</i>	4.3	3.8	none							Exline & Levi (1962)

* Two categories of relationship ('Assoc') are defined: 'K' is Kleptoparasite only, and 'KP' means that the guest may also capture the host. Some species of *Argyrodes* may be incorrectly categorised as 'Kleptoparasite only' because their predatory behaviour has not yet been observed.

** Taxonomy of *Argyrodes* follows Levi and Exline (1962) and thus *Argyrodes*, *Ariamnes* and *Rhomphaea* are not distinguished.

	Body length†		t statistic
	kleptoparasite only	kleptoparasite and predator	
♀ <i>Argyrodes</i>	2.9 ± 0.2 (14)	5.0 ± 1.1 (6)	3.41**
♂ <i>Argyrodes</i>	3.2 ± 0.2 (14)	3.7 ± 0.4 (5)	1.21
Dimorphism (♂/♀)	1.11 ± 0.05 (14)	0.82 ± 0.14 (5)	2.58*
Host	21.5 ± 2.6	6.7 ± 0.8 (5)	3.47**

TABLE 2: Differences in kleptoparasite and host body length according to whether the kleptoparasite does or does not also prey on their host.

† values are mean lengths ± SE (sample sizes). Values compared using t-test with pooled variance. Average host body size measures were obtained for *Argyrodes* that have multiple hosts. * $p < 0.05$; ** $p < 0.005$.

and Jackson, 1986; Jackson and Hallas, 1990). A potential cost of this foraging strategy is that the kleptoparasite may become prey to the host. At least one host species has a relatively effective defensive behaviour: when the predatory *Argyrodes* is detected, the host simply cuts the web thereby collapsing it and ensuring that the predator cannot proceed further (e.g. Eberhard, 1979b). Suter *et al.* (1989) report that female *F. pyramitela* can discriminate between conspecific males, prey items and predatory *A. trigonum*, apparently using chemical cues, and respond accordingly.

COMPARATIVE PATTERNS WITHIN ARGYRODES

What evolutionary sequences are responsible for the diversity of predatory specialisations in *Argyrodes*? Smith Trail (1980) stresses the importance of the kleptoparasites' ability to identify the vibratory signals generated by the host, thus allowing them to stalk and safely capture the host. However, kleptoparasites that also attempt to capture their hosts risk being captured themselves. Consequently they may be more likely to attempt to capture vulnerable hosts, such as those that are smaller (e.g. Smith Trail, 1980; Larcher and Wise, 1985), moulting (e.g. Vollrath, 1984), or even the spiderlings of the host (e.g. Whitehouse, 1986).

If relative body size is important in determining the outcome of attacking the host, then predatory species of *Argyrodes* may be larger than primarily kleptoparasitic species, or the former may tend to specialise on smaller hosts. These predictions are supported by comparative data of body length measures for 20 species of *Argyrodes* (see Table 1). Species of *Argyrodes* were divided into two groups, according to whether they preyed on their hosts: females of *Argyrodes* that are only kleptoparasitic are significantly smaller than those

that also prey on their hosts (Table 2). However, males of these two groups of species are not significantly different in body size (Table 2). *Argyrodes* that prey on their hosts also specialise on smaller hosts, compared with the size of the hosts of those species of *Argyrodes* that are only kleptoparasites (Table 2). These comparative data show that, as predicted, the difference in size between *Argyrodes* and its host is greater for those species that are primarily kleptoparasitic compared with those that are also predatory. These comparative data suggest that selection has either favoured larger body size for species that are both kleptoparasitic and prey on their hosts, or it has favoured a further reduction in body size in those species that are primarily kleptoparasitic. The latter argument is consistent with the view that kleptoparasitism is a specialised foraging strategy that evolved from a more general kleptoparasitic and predatory lifestyle (Vollrath, 1984).

The evolutionary sequence leading to the divergence of these two foraging strategies within *Argyrodes* is not known; one may have evolved from the other, or both may have diverged from a common web-building ancestor (see Whitehouse, 1986). Thus, it is not possible, without an accurate phylogeny, to establish whether selection has favoured an increase in body size with the predatory lifestyle, or a decrease in body size is associated with a kleptoparasitic lifestyle. Indeed, the species placed within the single genus *Argyrodes* by Exline and Levi (1962) have been placed by others into three genera; the *Ariannes*, the *Rhomphaea*, and the *Argyrodes*. In this classification, the *Ariannes* and *Rhomphaea* groups are primarily host-predators and the *Argyrodes* group are kleptoparasites (Whitehouse, 1987). Thus, the differences described above may be confounded by taxonomic associations (see below). Resolving some of these issues is most likely achieved by experimental manipulation of individuals within a species that shows both kleptoparasitic and predatory behaviour.

An additional pattern revealed by comparative analysis also deserves experimental investigation. The degree of sexual size dimorphism (male length/female length) covaries significantly with the foraging strategies of *Argyrodes*. Males are smaller than females in those species that prey on their host, consistent with patterns of size dimorphism in almost all other spiders (e.g. Elgar *et al.*, 1990; Elgar, 1991, 1992; Vollrath and Parker, 1992). However, males of those species of *Ar-*

Host taxa	Kleptoparasite*	Biology
Agelenidae		
<i>Agelena</i> (2), <i>Agelenopsis</i> , <i>Cambridgea</i> , <i>Stiphidion</i>	<i>Argyrodes</i> (4)	KP
Amaurobiidae		
<i>Badumna</i> (2)	<i>Simaetho</i> , <i>Argyrodes</i>	KK
<i>Amourobis</i>	<i>Oonops</i>	K
Araneidae		
<i>Araneus</i> (5), <i>Argiope</i> (4), <i>Cycloso</i> , <i>Cyrtophora</i> (2), <i>Gasteracantha</i> , <i>Leucauge</i> , <i>Mecynogea</i> , <i>Metozygio</i> , <i>Metepetra</i> , <i>Neoscona</i> , <i>Nephilo</i> (3), <i>Verrucoso</i>	<i>Argyrodes</i> (18)	KP
<i>Cyrtophora</i>	<i>Mysmenopsis</i> (2)	KK
Dipluridae		
<i>Allothele</i>	<i>Iselo</i>	K
<i>Diplura</i> , <i>Ischnothele</i>	<i>Mysmenopsis</i> (11)	KK
<i>Dipluro</i>	<i>Curimogua</i>	K
<i>Thelechoris</i>	<i>Kilifia</i>	K
Linyphiidae		
<i>Frontinella</i> (2), <i>Linyphio</i> , <i>Neriene</i>	<i>Argyrodes</i> (4)	KP
Phnclidae		
<i>Pholcus</i>	<i>Argyrodes</i> (2)	KK
<i>Pholcus</i> '	<i>Mysmenopsis</i>	K
Theridiidae		
<i>Achoeoroneo</i> , <i>Theridion</i> (3), <i>Anelosinus</i> , <i>Latrodectus</i>	<i>Argyrodes</i> (7)	KP
Uloboridae		
<i>Uloborus</i> , <i>Philoponella</i>	<i>Argyrodes</i> (4)	KP

TABLE 3: Summary of taxonomic distribution of spiders that are host of kleptoparasites (see Table 1 for further details). KP= Kleptoparasites and predators; K=kleptoparasites. * No. species in each genus in parentheses.

gyrodes that are primarily kleptoparasitic are generally larger than their conspecific females (see Table 2). What factors are responsible for this reversal of size dimorphism patterns within this group of spiders? One explanation is that competition between males for access to females may be more intense for kleptoparasitic spiders, and consequently sexual selection has favoured large male size in these species (see also Whitehouse, 1988b).

There is considerable variation in both the number of species that are host to each species of kleptoparasite and the number of kleptoparasite species found on each web-building host species (see also Vollrath, 1984, 1987b). For example, *Argyrodes cancellatus* are found on the webs of at least ten different host species from five families (see Table 3), while the orb-weaver *Nephila clavipes* is host to at least seven species

	Host range		t statistic
	Kleptoparasite only	Kleptoparasite and predator	
No. species*	18	6	
Family	1.6 ± 0.3	2.8 ± 0.7	1.89
Species	2.7 ± 0.7	3.5 ± 1.3	0.57

TABLE 4: Mean host-ranges of *Argyrodes* that are either only primarily kleptoparasitic or they also prey on their host. * refers to *Argyrodes*.

of *Argyrodes*. It is likely that both host-range and parasite-range will expand as more records become available. In contrast, many species appear to be host specific, with one species of kleptoparasite recorded from the web of only one species of host. For example, in certain Peruvian habitats, *Argyrodes ululans* is found only on the webs of the social spider *Anelosimus eximius*, despite considerable effort searching for this kleptoparasite on other potential hosts (Cangialosi, 1990a).

Vollrath (1984) argued that *Argyrodes* can be placed in two general categories; specialists that are host specific but behaviourally versatile, and generalists that invade the webs of many different species but use relatively few techniques to obtain food. Thus, Whitehouse (1988a) considers *Argyrodes antipodius* a specialist, primarily because its behaviour is versatile, and adults are found primarily on the webs of *Eriophora pustulosa*. Dichotomies like these can be misleading because both host-specificity and behavioural versatility are most likely continuous rather than discrete variables; *A. antipodius* is found on the webs of several other hosts (Table 1). Furthermore, host-specificity may also vary between populations, depending on the diversity and abundance of potential hosts in different populations. For example, *A. antipodius* in Whitehouse's (1988a) study may be found primarily on *Eriophora pustulosa* because that is the most common host in her New Zealand population.

The host range of *Argyrodes* may vary according to whether the species is both kleptoparasitic and predatory or whether it is only kleptoparasitic. Purely kleptoparasitic *Argyrodes* may escape host-detection through specialised behaviours, but these behaviours may be effective for relatively few host species. If so, the host ranges of primarily kleptoparasitic *Argyrodes* may be less than for species of *Argyrodes* that are also predatory. The comparative data provide little support for this prediction (Table 4); al-

though the host-range of primarily kleptoparasitic species is less than the range of predatory species, the difference is not statistically significant.

The results of these inter-specific comparative analyses within the genus *Argyrodes* should be interpreted cautiously. These patterns may be confounded by an association between foraging strategy and taxonomic affinity, and thus the differences in body size or host range may be due to other, unknown features that differ between these two groups. This possibility is especially relevant given the ambiguity of the taxonomic arrangement of this genus. Furthermore, some species of *Argyrodes* may be incorrectly assigned to primarily kleptoparasite status simply through lack of observations. Thus, the patterns may change when more data and/or a more accurate phylogeny become available. Nevertheless, the patterns suggest several interesting questions that could be resolved by an experimental approach.

HOST SPECIFICITY OF KLEPTOPARASITES

Both *Argyrodes* and *Mysmenopsis* belong to web-building families and thus are relatively close phylogenetically (Coddington and Levi, 1991). However, the range and taxonomic affinities of their hosts are substantially different (Table 1). *Argyrodes* have been recorded on the webs of 29 host genera from eight families (Agelenidae, Amaurobiidae, Araneidae, Linyphiidae, Pholcidae, Psecridae, Theridiidae, Uloboridae), and some species have many hosts (see above). In contrast, 11 of the 14 species of *Mysmenopsis* are found on diplurid hosts, with the remaining species found on *Cyrtophora* (Araneidae) and *Pholcus* (Pholcidae). A comparative analysis reveals a significant difference: every species of *Mysmenopsis* has only one host species, while the host range for *Argyrodes* is 2.7 (± 0.7 , $n=18$) species, or 1.6 (± 0.3) host families.

Why is *Mysmenopsis* more host-specific than *Argyrodes*? There are several possible explanations. First, kleptoparasitism may have evolved more recently in *Mysmenopsis* than in *Argyrodes*, and therefore the former kleptoparasite has had less time to expand its host range. Second, the present associations between *Mysmenopsis* and diplurids may have evolved from a common ancestor and subsequently speciated as host/kleptoparasite pairs. Consistent with this is Coyle and Meigs (1989) description of two sister species of kleptoparasites (*Mysmenopsis monticola* and *M. furtiva*) that live on the webs of a pair of un-

described allopatric *Ischnothele* morphs that also appear to be sister species. Third, diplurids may be more sensitive to web invaders than the hosts of *Argyrodes*, and thus the kleptoparasitic behaviours required to avoid detection by one host species are not appropriate for another. In this regard, it is noteworthy that *Argyrodes* are not known to invade diplurid webs, despite the broad taxonomic range of their hosts.

The relatively permanent nature of the host's web is a common characteristic of the hosts of all kleptoparasites (Table 1). Kleptoparasites that live on permanent webs may benefit by spending less time searching for new webs compared with those that are associated with hosts that frequently move their webs. However, it may not be the permanent structure of the web that is important, but rather the tenacity of the web site. For example, the large, nocturnal, Australian orb-weaver *Eriophora transmarina* builds a new web every evening and then destroys it the following dawn. Despite the temporary nature of its web, this spider is also host to many individual *Argyrodes*, probably because it has a high web-site tenacity (M. Herberstein, unpublished data).

MIMICRY BY SPIDERS

Many species of animals, including spiders, resemble other, unrelated species. These resemblances may be visual, chemical, behavioural or acoustic and are usually referred to as mimicry. There are many different types of mimicry, which has precipitated some controversy over its definition (e.g. Endler, 1981; Pasteur, 1982). Two general forms of mimicry are distinguished in this review: defensive mimicry and aggressive mimicry. In the former, the mimetic form is presumed to have evolved because the risk of predation (or parasitism) on the mimic is reduced as a result of its resemblance to the model. The lower mortality occurs because the receiver (the predator) does not usually prey on the model, and fails to distinguish between it and the mimic. Aggressive mimics resemble some feature of their prey species, thereby increasing the chance of capturing the prey model. Both forms of mimicry occur in several families of spiders.

The relationship between mimic, model and receiver is asymmetric; only the mimic benefits and any improvement in the mimic will be favoured rapidly by natural selection. Both the model and the receiver may lose, in defensive mimicry, through increased attack rate and lost

	Spider taxon		Ant Taxa		Source
		Family	Subfamily	Species	
ANT MIMICRY ONLY	<i>Castianeira dubium</i>	C1	Ponerinae	<i>Pachycondyla obscuricornis</i>	Reiskind (1977)
	<i>Mazax pax</i>	Co	Ponerinae	<i>Ectatomma ruidum</i>	Reiskind (1970)
	<i>Myrmecium bifasciatum</i>	Co	Formicinae	<i>Camponotus femoratus</i>	Oliveira (1988)
	<i>Myrmecium bifasciatum</i>	Co	Myrmicinae	<i>Megalomyrmex modesta</i>	Oliveira (1988)
	<i>Myrmecium</i> sp.	Co	Ponerinae	<i>Pachycondyla anidentata</i>	Oliveira (1988)
	<i>Myrmecium velutinum</i>	Co	Ponerinae	<i>Ectatomma lugens</i>	Oliveira (1988)
	<i>Myrmecotyplus cubanus</i>	Co	Formicinae	<i>Camponotus planatus</i>	Myers and Salt (1926)
	<i>Myrmecotyplus fuliginosus</i>	Co	Formicinae	<i>Camponotus planatus</i>	Jackson & Drummond (1974)
	<i>Myrmecotyplus reittemeyeri</i>	Co	Formicinae	<i>Camponotus sericeiventris</i>	Reiskind (1977)
	<i>Sphecotyplus niger</i>	Co	Ponerinae	<i>Pachycondyla villosa</i>	Oliveira (1988)
	<i>Micaria pulicaria</i>	Gn	Myrmicinae	<i>Acanthomyrmex niger</i>	Bristowe (1958)
	<i>Micaria</i> sp.	Gn	Myrmicinae	<i>Aphaenogaster beccarii</i>	Hingston (1927)
	<i>Micaria scintillans</i>	Gn	Formicinae	<i>Formica fusca</i>	Bristowe (1941)
	<i>Phrurolithus festivus</i>	Lio	Formicinae	<i>Lasius niger</i>	Bristowe (1941)
	<i>Phrurolithus minimus</i>	Lio	Formicinae	<i>Formica fusca</i>	Bristowe (1941)
	<i>Martella furva</i>	Sa	Formicinae	<i>Camponotus brevis</i>	Reiskind (1977)
	<i>Martella furva</i>	Sa	Formicinae	<i>Camponotus fastigatus</i>	Reiskind (1977)
	<i>Myrmaracline elongata</i>	Sa	Pseudomyrmecinae	<i>Tetrapanera anthracina</i>	Edmunds (1978)
	<i>Myrmaracline foenisex</i>	Sa	Formicinae	<i>Oecophylla longinoda</i>	Edmunds (1978)
	<i>Myrmaracline formicaria</i>	Sa	Formicinae	<i>Formica rufa</i>	Bristowe (1941)
	<i>Myrmaracline legon</i>	Sa	Formicinae	<i>Camponotus acvapinensis</i>	Edmunds (1978)
	<i>Myrmaracline lupata</i>	Sa	Formicinae	<i>Polyrhachis</i>	Jackson (1986)
	<i>Myrmaracline parallela</i>	Sa	Ponerinae	<i>Pachycondyla carinulata</i>	Reiskind (1977)
	<i>Myrmaracline parallela</i>	Sa	Ponerinae	<i>Pachycondyla striatinodis</i>	Reiskind (1977)
	<i>Myrmaracline plataleoides</i>	Sa	Formicinae	<i>Oecophylla smaragdina</i>	Mathew (1954)
	<i>Myrmaracline</i> sp.	Sa	Formicinae	<i>Polyrhachis simplex</i>	Hingston (1927)
	<i>Myrmaracline</i> sp.	Sa	Formicinae	<i>Prenolepis longicornis</i>	Hingston (1927)
	<i>Myrmaracline</i> sp.	Sa	Myrmicinae	<i>Pheidole indica</i>	Hingston (1927)
	<i>Sarinda linda</i>	Sa	Formicinae	<i>Camponotus planatus</i>	Jackson & Drummond (1974)
	<i>Synageles occidentalis</i>	Sa	Formicinae	<i>Myrmica americana</i>	Cutler (1991)
	<i>Synageles occidentalis</i>	Sa	Formicinae	<i>Lasius alienus</i>	Cutler (1991)
	<i>Synageles venator</i>	Sa	Formicinae	<i>Lasius niger</i>	Engelhardt (1970)
	<i>Synemosyna</i> sp.	Sa	Pseudomyrmecinae	<i>Pseudomyrmex mexicanus</i>	Reiskind (1977)
	<i>Synemosyna americana</i>	Sa	Pseudomyrmecinae	<i>Pseudomyrmex boopis</i>	Reiskind (1977)
	<i>Synemosyna aurantiaca</i>	Sa	Pseudomyrmecinae	<i>Pseudomyrmex</i>	Oliveira (1988)
	<i>Synemosyna smithi</i>	Sa	Pseudomyrmecinae	<i>Pseudomyrmex elongata</i>	Myers and Salt (1926)
<i>Synemosyna smithi</i>	Sa	Pseudomyrmecinae	<i>Pseudomyrmex flavida</i>	Myers and Salt (1926)	
<i>Zuniga laela</i>	Sa	Formicinae	<i>Camponotus femoratus</i>	Oliveira (1988)	
<i>Zunigo magna</i>	Sa	Ponerinae	<i>Pachycondyla villosa</i>	Oliveira (1988)	
<i>Anatea formicaria</i>	Td	Myrmicinae	<i>Chelaner cracceiventre</i>	Reiskind and Levi (1967)	
<i>Dipozena</i>	Td	Myrmicinae	<i>Pheidole indica</i>	Hingston (1927)	

TABLE 5 (part). Taxonomic distribution of spiders that mimic ants, including those that also prey on the model. * spiders observed with dead ants. Family abbreviations given in Table 1.

food respectively (see Endler, 1991), and natural selection will favour models that have less resemblance to the mimic (although the strength of this selection will depend on the frequency with which the model is attacked). The degree of resemblance between model and mimic that evol-

ves will depend upon the benefits to the mimic and the costs of mimicry to the model. The costs to the model in aggressive mimicry are more complicated, and depend upon whether the model and the receiver (in this case, the potential prey) is the same individual.

	Spider taxon		Ant Taxa		Source
		Fam	Subfamily	Species	
ANT MIMIC AND PREDATOR	<i>Castianeira</i> sp.	Cl	Formicinae	<i>Camponotus paria</i>	Hingston (1927)
	<i>Cosmophasis</i> sp. 1	Sa	Formicinae	<i>Camponotus detritus</i>	Curtis (1988)
	<i>Cosmophasis</i> sp. 2	Sa	Formicinae	<i>Camponotus fulvopilosus</i>	Curtis (1988)
	<i>Myrmarachne</i> sp.	Sa	Formicinae	<i>Camponotus compressus</i>	Hingston (1927)
	<i>Tutelina similis</i>	Sa	Formicinae	<i>Camponotus</i>	Wing (1983)
	Not identified	Th	Formicinae	<i>Oecophylla smaragdina</i>	Cooper et al. (1990)
	<i>Ameyciaea albomaculata</i>	Tm	Formicinae	<i>Oecophylla smaragdina</i>	Cooper et al. (1990)
	<i>Ameyciaea forticeps</i>	Tm	Formicinae	<i>Oecophylla smaragdina</i>	Hingston (1927); Mathew (1954)
	<i>Bucranium</i>	Tm	Myrmicinae	<i>Cephalotes (= Cryptocerus)</i>	Bristowe (1941)
	<i>Aphanochilus rogersi</i>	Ap	Myrmicinae	<i>Zacryptocerus pusillus</i>	Oliveira and Sazima (1984)
	<i>Habronestes bradleyi</i>	Zo	Dolichoderinae	<i>Iridomyrmex purpureus</i>	R. Allan (pers. comm.)
	<i>Zodarion</i>	Zo	Myrmicinae	<i>Messor barbarus</i>	Hingston (1927)

Table 5. continued

VISUAL MIMICRY: SPIDERS OF ANTS

Spiders that resemble ants are an especially intriguing form of mimicry that is poorly understood. Many of these spiders not only have an extraordinary physical resemblance with their ant models, but also exhibit particular behaviours that improves the illusion remarkably. Ant-mimics, represented in at least six families of spiders and mimicking the four major subfamilies of ants (Table 5), fall into two categories: those that appear to have little behavioural interaction with the ants and generally avoid contact with them; and those spiders that specialise on capturing and eating their ant models. There are no clear taxonomic affiliations between the species of spider mimics and the species of ant models; ponerine, myrmecine and formicine ants are models for both clubionid, salticid and other spiders. Nevertheless, certain species of ants appear to be models for spiders more frequently than others. For example, seven species of *Camponotus* are models to spider mimics and one species, *C. femoratus*, is a model for two corinnids (*Myrmecium*) and the salticid *Zuniga*; five species of the ponerine genus *Pachycondyla* are models for five different spiders, and the weaver ant *Oecophylla smaragdina* is a model for three species from Australia and India. It is not obvious why spiders mimic these genera of ants more frequently than others.

Some species of spiders mimic more than one species of ant. For example, the clubionid *Castianeira rica* resembles species of both ponerine and myrmecine ants and the different mimetic forms depend upon developmental changes, colour variation in adult females, and sexual dimorphism (Reiskind, 1970). Male *C. rica* resemble *Atta* and *Odontomachus*, while females

resemble moderately large ponerines that are within the spiders' colour range. Furthermore, different instars of these spiders mimic ant models of equivalent size; thus the small, black early instars mimic small myrmecine ants, while the older instars resemble medium sized attine ants. Such a close degree of resemblance at different stages in the spiders' development suggests that the selection pressure favouring mimicry is very strong.

Ant mimicry can provide at least three benefits, depending upon whether the spiders prey on their ant models. These benefits include protection from various predators, improved predatory success on the ant prey, and both. Ant-mimics that apparently do not prey on their models are mostly salticids, corinnids and a few gnaphosids (Table 5). Mimics that prey on their models are mostly represented by thomisids and zodarids, although there are also a few records of theridiids, corinnids and salticids (Table 5). The record for the salticid species *Myrmarachne* (Hingston, 1927) is unusual and unlikely to be typical because other species of this large, ant-mimicking genus do not routinely prey on their model ants (e.g. Edmunds, 1978). Only a few genera of salticids are clearly regular ant-predators (e.g. Jackson and van Olphen, 1991, 1992). The theridiid *Dipoena* resembles the de-capitated head of a dead ant which are found in the refuse heap of the ant nest. Hingston (1927) suggests that mimicry in this species is aggressive because it allows the spider to live in the nest of the ants on whom it may prey. However, predation on these ant hosts by *Dipoena* was not observed.

Perhaps the most vexing question concerning defensive ant mimicry by spiders is establishing the identity of the receiver (i.e. the predator or

Spider		Ant		Source
Species	Family	Subfamily	Species	
<i>Deinopis longipes</i>	De	not specified		Robinson & Robinson (1971)
<i>Chryssilla lauta</i>	Sa	not specified		Jackson & van Olphen (1992)
<i>Corythalio conosa</i>	Sa	not specified		Jackson & van Olphen (1991)
<i>Hobrocestum pulex</i>	Sa	Formicinae	<i>Lasius</i> sp., <i>Prenolepis</i> sp.	Cutler (1980)
<i>Hobrocestum pulex</i>	Sa	Ponerinae	<i>Ponera pennsylvanica</i>	Cutler (1980)
<i>Natta</i> sp.	Sa	not specified		Jackson & van Olphen (1992)
<i>Notto rufopicta</i>	Sa	not specified		Jackson & van Olphen (1992)
<i>Pystira orbiculato</i>	Sa	not specified		Jackson & van Olphen (1991)
<i>Siler semiglaucus</i>	Sa	not specified		Jackson & van Olphen (1992)
<i>Corythalio conosa</i>	Sa	not specified		Edwards <i>et al.</i> (1975)
<i>Euryopis colifornica</i>	Td	Formicinae	<i>Componotus</i>	Porter & Eastmond (1982)
<i>Euryopis coki</i>	Td	Myrmicinae	<i>Pogonomyrmex</i>	Porter & Eastmond (1982)
<i>Euryopis funebris</i>	Td	Formicinae	<i>Componotus costaneus</i>	Carico (1978)
<i>Latrodectus hesperus</i>	Td	Myrmicinae	<i>Pogonomyrmex rugosus</i>	MacKay (1982)
<i>Latrodectus pollidus</i>	Td	Myrmicinae	<i>Monomorium semirufus</i>	MacKay (1982)
<i>Steotodo fulvo</i>	Td	Myrmicinae	<i>Pogonomyrmex bodius</i>	Hölldobler (1971)
<i>Achoearoneo</i> sp.	Td	Formicinae	<i>Oecophyllo smaragdino</i>	Cullen (1991)
<i>Soccodomus formivorus</i>	Tm	Dolichoderinae	<i>Iridomyrmex</i>	McKeown (1952)
<i>Strophius nigriconis</i>	Tm	Formicinae	<i>Camponotus crossus</i>	Oliveira & Sazima (1985)
<i>Zodiorion frenatum</i>	Zo	Formicinae	<i>Cataglyphis bicolor</i>	Harkness (1976)

TABLE 6: Spiders that specialise on ant prey but are not ant-mimics. Family abbreviations given with Table 1.

parasitoid). Despite widespread reports and descriptions of ant-mimicry by spiders, few studies have addressed this question quantitatively. The visual nature of ant-mimicry suggests that the spiders are gaining protection from visual enemies, including birds (e.g. Belt, 1874; Engelhardt, 1970), wasps (e.g. Edmunds, 1993) and other spiders (e.g. Cutler, 1991). It is unlikely that the visual resemblance to ants provides the spider mimics with protection from either their ant models or other species of ants, because ants perceive the environment primarily by chemical, rather than visual cues (see Hölldobler and Wilson, 1990). Furthermore, many spiders that are either specialist predators of ants (see Table 6) or live in close proximity with ants (Table 7) are not necessarily visual mimics.

Most of the diet of many spiders are other spiders (e.g. Bristowe, 1941, 1958; Reichert and Luczak, 1982; Nentwig, 1987). In contrast, ants are not a common prey item for most spiders, although a few spiders are specialist predators of ants (see Table 6). Thus, ant mimicry may provide some degree of protection from other spiders. Experimental evidence of this possibility is provided by Cutler (1991), who examined whether ant-mimicry in the salticid *Synageles occidentalis*, a mimic of the ant *Myrmica americana*, reduces the risk of predation by two

other spiders *Tibellus* (Philodromidae) and *Phidippus* (Salticidae). These spiders do not feed on the ant *M. americana*, but more importantly they were less likely to attempt to capture the mimic *S. occidentalis* than immature *Phidippus* (that are not ant mimics).

Spiders are also prey to a variety of other invertebrates, especially pompilid and sphecid wasps (e.g. Coville, 1987), and acrocerid dipterans (e.g. Schlinger, 1987). These parasitoids are primarily visual hunters and many myrmecophilous arthropods gain protection against these enemies by associating with ants (e.g. Hölldobler and Wilson, 1990). Thus, ant-mimicry may reduce the risk of predation by sphecid and pompilid wasps. Edmunds (1993) provides qualitative data suggesting that ant-mimics *Myrmarachne* are less likely to be taken by the predatory wasp *Pison xanthopus* than might be expected if this wasp was indiscriminate in its choice of prey. Finally, it is interesting to note that no species of lycosid have been reported as ant-mimics (see Table 5), perhaps because these spiders are generally nocturnal foragers and are also seldom victim to sphecid wasps (see Coville, 1987).

BEHAVIOURAL MIMICRY: COURTSHIP VIBRATIONS

Some spiders are renowned for preying exclusively on other spiders. Notable among these

Spider		Ant		Source
Species	Family	Subfamily	Species	
<i>Tetrilus arientinus</i>	Ag	Formicinae	<i>Formica</i>	Bristowe (1958)
<i>Eiica puna</i>	Gn	Formicinae	<i>Camponotus inca</i>	Noonan (1982)
<i>Acurtauchenius scurrilis</i>	Lin	Formicinae	<i>Tetramorium caespitum</i>	Bristowe (1958)
<i>Cochlenbulus formicarius</i>	Lin	Formicinae	<i>Formica obscuripes</i>	Dondale & Redner (1972)
<i>Evansia merens</i>	Lin	Formicinae	<i>Formica fusca</i>	Bristowe (1958)
<i>Masoncus</i>	Lin	Formicinae	<i>Pogonomyrmex</i>	Porter (1985)
<i>Thyreosthenius biovatus</i>	Lin	Formicinae	<i>Formica rufa</i>	Bristowe (1958)
<i>Pkrurolithus</i>	Lio	Formicinae	<i>Crematogaster</i>	Porter (1985)
<i>Myandra</i>	Pro	not specified		Main (1976)
<i>Cotinusa</i>	Sa	Dolichodennae	<i>Tapinoma melanocephalum</i>	Shepard & Gibson (1972)

TABLE 7: Spiders that have been found within or adjacent to the nests of ants. Family abbreviations given with Table 1.

are the mimetid or pirate spiders that invade the webs and attack the owners of other species of spiders (e.g. Bristowe, 1941). Many of these spiders are aggressive mimics. For example, the mimetid pirate spiders *Mimetus* and *Ero* wait at the periphery of the web of the social spider *Anelosimus studiosus* (Brach, 1977). The mimetids then pluck on the web thereby attracting a host spider that is then captured and eaten. The salticid *Portia* is also well known for its ability to mimic the struggles of prey ensnared in the web of other spiders. The investigating host is then captured by *Portia* (Jackson and Hallas, 1990).

Some species of *Portia* also mimic the male courtship behaviour of their prey species; a behaviour that increases their chances of capturing the unsuspecting female (Jackson and Hallas, 1986). If prey populations suffer high frequencies of this form of mimicry, then *Portia* may act as a selection pressure favouring improved discriminatory abilities in the prey, thereby establishing an evolutionarily dynamic 'arms race' (*sensu* Dawkins and Krebs, 1979). Evidence of this form of frequency dependent selection is provided by Jackson and Wilcox (1990, 1993), in their study of the predatory-prey relationship between two Australian salticids, *Portia fimbriata* and *Euryattus* sp.

Euryattus females live in a nest comprising a rolled-up leaf, suspended from rock ledges and tree trunks by silk gylines. *Portia fimbriata* is a versatile predator of many salticids and in a Queensland population, it preys on female *Euryattus* sp. using vibratory displays that apparently mimic the courtship behaviour of *Euryattus* males. This behaviour lures *Euryattus* females from their nest, and they are subsequently attacked by *P. fimbriata*. This

specialised form of predation by *P. fimbriata* may be responsible for the improved ability of *Euryattus* to recognise and defend itself from *P. fimbriata*, compared with other salticids. For example, *Euryattus* recognises *P. fimbriata* as a potential predator, unlike another prey species *Jacksonoides queenslandica*. Interestingly, this recognition ability is not present in another population of *Euryattus* in which *P. fimbriata* are absent. Experimental trials reveal that *P. fimbriata* attacks and captures these 'naïve' spiders more frequently than spiders from the population that is exposed to *P. fimbriata* (Jackson and Wilcox, 1993). It is still not clear whether the two populations of *Euryattus* are conspecifics or represent two different species. The more distantly related the two populations, the less likely that the differences in behaviour are the result of the presence or absence of *P. fimbriata*. Nevertheless, it appears to be a fascinating example of how the foraging behaviour of a predator has apparently acted as a selection pressure influencing the defensive behaviour of its prey.

CHEMICAL MIMICRY: MOTHS AND ANTS

Spiders produce a variety of chemicals that function to attract conspecifics. Female spiders from many different families produce pheromones that attract members of the opposite sex (e.g. Lopez, 1987; Pollard *et al.*, 1987), and Evans and Main (1993) show experimentally that pheromones may be important for maintaining social cohesion in social spiders. Several taxa of spiders are capable of inter-specific chemical communication, of which the most familiar is the remarkable form of chemical mimicry by bolas spiders (see Stowe, 1986, 1988 for extensive reviews). Bolas spiders, comprising several genera within the Araneidae, do not construct

orb-webs but instead swing at their prey a bolas (a droplet of adhesive) attached to the end of a silk thread. Bolas spiders are aggressive mimics and prey exclusively on male moths; the spiders produce a chemical substance that mimics the sex pheromone of its moth prey species (see Eberhard, 1977, 1980; Yeargan, 1988; Stowe, 1986, 1988; Stowe *et al.*, 1987). The exact source of the prey attractant compounds is not known, but is likely to be emitted from the spider (Stowe *et al.*, 1987). The evolution of this specialised foraging technique is particularly intriguing because it involves two phases; the first comprises the production of moth-attracting chemicals (see also Horton, 1979), and the second is the adoption of a specialised use of silk together with the loss of the orb-web. Interestingly, anecdotal observations suggest that the spider swings the bolas in response to vibratory signals generated by the flying moths (Main, 1976).

The mate location mechanism of at least seven families of moths are exploited by bolas spiders, but the range of moth prey species captured by each species of bolas spider varies (Stowe, 1986, 1988; Stowe *et al.*, 1987). Some spiders capture only one species of moth, while *Mastophora conigera* is capable of capturing at least nineteen moth species (Stowe *et al.*, 1987). There are no obvious taxonomic affinities between the different groups of bolas spider and their moth prey species (Stowe, 1986, 1988). The variation in bolas spider prey-specificity is likely to be related to the bio-geographic distribution of potential moth prey, the chemical compounds produced by the spiders and the chemicals used as moth sex-attractants. Furthermore, some compounds that attract certain species of moth may inhibit attraction of other moths (Stowe *et al.*, 1987).

Since araneid spiders are capable of chemical mimicry of moths, it is not unreasonable to expect that ant-mimicking spiders may be capable of producing chemical compounds that 'appease' ants. Many species of invertebrate myrmecophiles produce chemicals that mimic ant communication chemicals (see Hölldobler and Wilson, 1990). The production of these chemicals can reduce the risk of the ants attacking the myrmecophiles. One group of spiders that are likely to be capable of chemical mimicry are those that live in ant nests (see Table 7). Little is known about these spiders, but some earlier reports may have mistakenly recorded them living in ant nests, rather than adjacent to the nest (see Bristowe, 1941). It is not clear whether these spiders prey on the ant larvae within the ant nest,

or simply take advantage of a safe refuge. Whatever the reason, it is unlikely that they could remain in or near ant nests without some chemical protection, because ants rarely tolerate foreign nest intruders. Porter (1985) provided qualitative evidence for the presence of ant recognition pheromones by introducing myrmecophilous spiders *Masoncus* into the nests of different *Pogonomyrmex* ants. *Masoncus* were not attacked if they were re-introduced into their original nests, but the spiders were attacked and killed within minutes if they were placed in the nest of foreign *Pogonomyrmex* or other species of ants. It is not known whether these spiders actively produce the appropriate pheromones, or whether they simply adopt it from the substrate of the nest.

The predatory behaviour of two Australian spiders may also involve chemical mimicry. The Australian basket-web spider *Saccodomus formivorus* (Thomisidae) builds a basket-like web that appears to attract wandering *Iridomyrmex* ants that may venture into the basket web (McKeown, 1952). The spider also taps the ant with its legs, that may further mimic ant communication, and eventually captures the unsuspecting ant. It remains to be seen if *S. formivorus* webs capture only *Iridomyrmex* ants, and whether the ants are actively attracted to the basket-web. The extraordinary predatory relationship between an undescribed theridiid and its weaver ant *Oecophylla smaragdina* prey (see Cooper *et al.*, 1990) may also represent an example of the use of chemical mimicry. This theridiid constructs a web made of several strands of silk suspended between vegetation and additional strands that are anchored to the substrate below. The anchor part is a small white bead of silk that is very attractive to the ants. If the web is complete and an ant bites the silk it is catapulted into the web above, where it is captured by the spider. The bead of silk is often placed near ant 'highways' and can sometimes attract the attention of many individual *O. smaragdina* that all attempt to bite the silk.

MUTUALISTIC ASSOCIATIONS

There are few examples of mutualistic associations between species of spiders or even between spiders and other organisms. This is surprising, given the widespread occurrence of mutualistic associations in other taxa (e.g. Boucher *et al.*, 1982; Smith and Douglas, 1987; Hölldobler and Wilson, 1990), but may reflect the predatory nature of spiders. Tietjen *et al.* (1987) describe an

interesting example of a mutualistic association involving the social spiders *Mollos gregalis*. These spiders do not remove the remains of prey from their nest, and this debris becomes a nutrient base for various yeasts. The odour of these yeasts is apparently attractive to various flies, that settle on the prey carcasses and are then captured by the spiders. The association is likely to be mutualistic because the spiders provide food for the yeast and the yeast's presence attracts food for the spider.

The relationship between spiders that live in ants' nests and their ant hosts may also be mutualistic for some species. For example, Shepard and Gibson (1972) found myrmecophilous salticid spiders of the genus *Cotinusa* in 61% of 50 nests of the dolichoderine ant *Tapinoma melanocephalum*. Interestingly, ant nests with *Cotinusa* had more brood per nest, more workers per nest and more brood per worker than those nests without *Cotinusa*. Unfortunately, these differences were not examined statistically, and the greater numbers of ants and brood in the nests with *Cotinusa* may be due to the larger size of the former nests. Nevertheless, Shepard and Gibson (1972) suggest that the spider uses the ant nest as a foundation for the construction of its web, and in return provides the ants with some protection from predators or parasites.

PSECHRUS AND *PHILOPONELLA*

Many species of orb-weaving spiders in the genus *Philoponella* (Uloboridae) build their webs within the barrier webs of other araneid, theridiid, agelenid and psechrid spiders (Struhsaker, 1969; Lubin, 1986). These associations were thought to be commensal; *Philoponella* has a place to build a web, but it was assumed that their presence has little effect on the host spider (e.g. Lubin, 1986).

In Madang Province, Papua New Guinea a species of *Philoponella* builds webs between the threads of the tangle web of a large psechrid *Psechrus argentatus*. Not all *Psechrus* webs have *Philoponella*, but as many as 15 males and females can be found on a single host web. Like many small uloborids, *Philoponella* is a communal spider, with several orb-webs sharing support threads. A theridiid *Argyrodes fissifrons* also patrols the barrier web but is never found on the sheet web of the host spider. The number of both *A. fissifrons* and *Philoponella* on a single host web is positively correlated with the size of the host.

The relationship between *P. argentatus* and *Philoponella* appears to be mutualistic (Elgar, unpublished). The growth rate of *P. argentatus*

was significantly reduced following experimental removal of both *A. fissifrons* and *Philoponella* from the barrier-web. The lower growth rate during the ten day experimental period may represent a potential reproductive loss of around 30 eggs (estimated from the weights of egg masses). *P. argentatus* probably benefits by increased capture rates as a result of the increased area of tangle web generated by the webs of *Philoponella*, in a way analogous to the webs of some social spiders (see Struhsaker, 1969; Uetz, 1988). The additional webs may increase the probability of arresting insects that then drop into the sheet web, without being caught in the orb-web of *Philoponella*. It seems unlikely that *P. argentatus* benefits from the presence of *A. fissifrons*. In fact, *A. fissifrons* is more likely to have a negative effect on the host because it feeds on prey items caught in the barrier web and also may prey on *Philoponella*: on two occasions, *A. fissifrons* were seen feeding on *Philoponella*, consistent with other reports of the foraging behaviour of this species (see Table 1).

SOME CONCLUSIONS AND PROSPECTS

The relationship between kleptoparasitic *Argyrodes* and their hosts has been extensively examined, yet the effects of the association on the fitness components of either *Argyrodes* or its host are presently unquantified. Consequently, it may be inappropriate to call these species kleptoparasites because (a) they may not take prey that the host would otherwise feed on and (b) their hosts may not suffer a fitness cost. Of course, many other well documented host-parasite systems similarly fail to quantify the fitness effects of the presumed parasite (see Toft *et al.*, 1991). Nevertheless, circumstantial evidence that the presence of *Argyrodes* has influenced the biology of at least a few host species suggests that kleptoparasitism is an evolutionarily dynamic relationship. Comparative analyses reveal interesting differences in the biology of kleptoparasites that do, or do not, also prey on their host. However, there are no obvious explanations for the evolution of this behaviour.

There are interesting parallels between chemical mimicry by the bolas spider and vibratory mimicry by the salticid *Portia*; both are examples of aggressive mimicry in which the mimic exploits the mate-attracting mechanism of the model. They also illustrate the broad spectrum of sensory mechanisms that are exploited and the range of phylogenetic similarity between model

and mimic. The models are clearly disadvantaged by the mimics, and selection is likely to favour mechanisms that allow the victims to distinguish between their conspecific mates and the spider predators. There is some evidence of this selection for *Euryattus*, the model of *Portia*, but there are no data on the impact of bolas spiders on their model moth populations (but see Yeargan, 1988), nor is it known whether the ability of male moths to discriminate between conspecific female pheromones and bolas spider mimics has changed. One difference between these two mimicry systems is that the victims of *Portia* are female, but the victims of bolas spiders are male. This difference may have implications for the relative strength of selection in these types of aggressive mimicry, and the degree to which the model and mimic have undergone an evolutionary arms race.

Defensive mimicry of ants by spiders is taxonomically widespread but has received little experimental attention, compared with studies of other invertebrate taxa (e.g. McIver, 1987). In almost all cases the receiver is not identified and the fitness cost to the ants, as a result of defensive mimicry by these spiders, has not been quantified. Nevertheless, the degree of visual mimicry in many spiders suggests that there has been strong selection for this form of protection against predators. The inter-specific variation in the degree of resemblance between spider mimics and their ant models suggests an evolutionary process reflecting differences in the discriminatory abilities of the receivers. These differences may also reflect the frequency with which the spiders and ants co-occur, and the kind of substrate on which both are found. Finally, ant mimicry by spiders that also prey on their models begs the question of whether specialisation on ant prey followed ant mimicry, or vice-versa.

Mutualisms involving spiders have received little attention, compared with other inter-specific associations. There are several explanations: the Araneae may be characterised by an absence of mutualisms; these mutualisms simply have not been detected; or non-mutualistic associations may even have been incorrectly inferred. For example, the impetus of my study of *Psecrus*, *Philoponella* and *Argyrodes* was to reveal the fitness costs to the host of what appeared to be a kleptoparasitic relationship. The correct nature of the relationship between the species was only revealed experimentally, and this is likely to be true of many other inter-specific associations described in this review. But

irrespective of the true nature of these relationships, inter-specific associations involving spiders provide a rich seam of biological systems that pose a variety of fascinating questions.

ACKNOWLEDGEMENTS

I am very grateful for the critical comments and discussion provided by Rachel Allan, Jonathan Coddington, William Eberhard, Malcolm Edmunds, Theo Evans, Mary Whitehouse and especially Robert Jackson and Fritz Vollrath; not all agree with me, but their advice is appreciated. Thanks also to Rachael Bathgate for helping compile the kleptoparasite data-base; Fritz Vollrath for the Zusammenfassung; Mark Harvey, Bill Humphreys and Barbara York Main for their encouragement; and the W.V. Scott Fund, University of Melbourne and Australian Research Council (grant A19130739) for financial support.

LITERATURE CITED

- BAERT, L. 1990. Mysmenidae (Araneae) from Peru. *Bulletin de l'Institut Royal Scientifique de Belgique* 60: 5-18.
- BAPTISA, R. 1988. On *Mysmenopsis* (Mysmenidae) a kleptoparasite of Pholcidae. *American Arachnology* 38: 4.
- BELT, T. 1874. 'The Naturalist in Nicaragua'. (John Murray: London).
- BERRY, J.W. 1987. Notes on the life history and behavior of the communal spider *Cyrtophora moluccensis* (Dobson) (Araneae, Araneidae) in Yap, Caroline Islands. *Journal of Arachnology* 15: 309-319.
- BOUCHER, D.H., JAMES, S. and KEELER, K.H. 1982. The ecology of mutualism. *Annual Review of Ecology and Systematics* 13: 315-347.
- BRACH, V. 1977. *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasociality in theridiid spiders. *Evolution* 31: 154-161.
- BRISTOWE, W.S. 1941. 'The Comity of Spiders'. Volume 2. (Ray Society: London).
1958. 'The World of Spiders'. (Collins: London.)
- BRODIE, E.D., III & BRODIE, E.D. 1991. Evolutionary response of predators to dangerous prey: reduction of toxicity of newts and resistance of garter snakes in island populations. *Evolution* 45: 221-224.
- BUSKIRK, R.E. 1981. Sociality in the Arachnida. Pp. 281-367. In: H.R. Hermann (ed.). 'Social Insects'. Volume II. (Academic Press: New York).
- CANGIALOSI, K.R. 1990a. Life cycle and behaviour of the kleptoparasitic spider, *Argyrodes ululans* (Araneae, Theridiidae). *Journal of Arachnology* 18: 347-358.
- 1990b. Social spider defense against klep-

- toparasites. *Behavioral Ecology and Sociobiology* 27: 49-54.
1991. Attack strategies of a spider kleptoparasite; effects of prey availability and host colony size. *Animal Behaviour* 41: 639-647.
- CARICO, J.E. 1978. Predator behaviour in *Euryopis funebris* (Hentz) (Araneae: Theridiidae) and the evolutionary significance of web reduction. Symposium of the Zoological Society of London 42: 51-58.
- CODDINGTON, J.A. & LEVI, H.W. 1991. Systematics and the evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* 22: 565-592.
- COOPER, D., WILLIAMSON, A. & WILLIAMSON, C. 1990. Deadly deception. *Geo* 12(1): 87-95.
- COVILLE, R.E. 1987. Spider-hunting sphecid wasps. Pp. 309-318. In: W. Nentwig (ed.), 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).
- COYLE, F.A. & MEIGS, T.E. 1989. Two new species of kleptoparasite *Mysmenopsis* (Araneae, Mysmenidae) from Jamaica. *Journal of Arachnology* 17: 59-70.
- COYLE, F.A., O'SHIELDS, T.C. & PERLMUTTER, D.G. 1991. Observations on the behaviour of the kleptoparasitic spider *Mysmenopsis furtiva*. *Journal of Arachnology* 19: 62-66.
- CULLEN, E. 1991. Observations on an ant-eating theridiid spider. *Australasian Arachnology* 42: 3-6.
- CURTIS, B.A. 1988. Do ant-mimicking *Cosmophasis* prey on their *Camponotus* models? *Cimbebasia* 10: 67-70.
- CUTLER, B. 1980. Ant predation by *Habrocestum pulex* (Hentz) (Araneae: Salticidae). *Zoologischer Anzeiger, Jena* 204: 97-101.
1991. Reduced predation on the antlike jumping spider *Synageles occidentalis* (Araneae: Salticidae). *Journal of Insect Behavior* 4: 401-407.
- DAVIES, N.B., BOURKE, A.F.G. & BROOKE, M. DE L. 1989. Cuckoos and parasitic ants: interspecific brood parasitism as an evolutionary arms race. *Trends in Ecology and Evolution* 4: 274-278.
- DAWKINS, R. & KREBS, J.R. 1979. Arms races between and within species. *Proceedings of the Royal Society of London B* 205: 489-511.
- DONDALE, C.D. & REDNER, J.H. 1972. A synonym proposed in *Perimones*, a synonym rejected in *Walckenaera*, and a new species described in *Cochlembolus* (Araneida: Erigonidae). *Canadian Entomologist* 104: 1643-1647.
- EBERHARD, W.G. 1977. Aggressive chemical mimicry by a bolas spider. *Science* 198: 1173-1175.
- 1979a. *Argyrodes attenuatus* (Theridiidae): a web that is not a snare. *Psyche* 86: 407-413.
- 1979b. Predatory behaviour of an assassin spider, *Chorizopes* sp. (Araneidae), and the defensive behaviour of its prey. *Journal of the Bombay Natural History Society* 79: 522-524.
1980. The natural history and behavior of the bolas spider *Mastophora dizzydeani* sp. n. (Araneae). *Psyche* 87: 143-169.
1986. Web building behavior of anapid, symphytonathid and mysmenid spiders (Araneae). *Journal of Arachnology* 14: 339-356.
- EDMUNDS, M. 1978. On the association between *Myrmarachne* spp. (Salticidae) and ants. *Bulletin of the British Arachnological Society* 4: 149-160.
1993. Does mimicry of ants reduce predation by wasps on salticid spiders? *Memoirs of the Queensland Museum* 33: 507-512.
- EDWARDS, G.B., CARROLL, J.F., WHITCOMB, W.H. 1975. *Stoides aurata* (Araneae: Salticidae), a spider predator of ants. *Florida Entomologist* 57: 337-346.
- ELGAR, M.A. 1989. Kleptoparasitism: a cost of aggregating for an orb-weaving spider. *Animal Behaviour* 37: 1052-1054.
1991. Sexual cannibalism, size dimorphism and courtship behavior in orb-weaving spiders (Araneae). *Evolution* 45: 444-448.
1992. Sexual cannibalism in spiders and other invertebrates. Pp. 129-156. In: M.A. Elgar and B.J. Crespi (eds), 'Cannibalism: ecology and evolution among diverse taxa'. (Oxford University Press: Oxford).
- ELGAR, M.A. & GODFRAY, H.C.J. 1987. Sociality and sex ratios in spiders. *Trends in Ecology and Evolution* 2: 6-7.
- ELGAR, M.A., GHAFER, N. & READ, A. 1990. Sexual dimorphism in leg length among orb-weaving spiders: a possible role for sexual cannibalism. *Journal of Zoology, London* 222: 455-470.
- ELGAR, M.A., POPE, B. & WILLIAMSON, I. 1983. Observations on the spatial distribution and natural history of *Cyrtophora hirta* (L. Koch) (Araneae: Araneidae). *Bulletin of the British Arachnological Society* 6: 83-87.
- ENDLER, J.A. 1981. An overview of the relationships between mimicry and crypsis. *Biological Journal of the Linnean Society* 16: 25-31.
1986. 'Natural Selection in the Wild'. (Princeton University Press: Princeton).
1991. Interactions between predators and prey. Pp. 169-196. In: J.R. Krebs and N.B. Davies (eds), 'Behavioural Ecology: an Evolutionary Approach'. (Blackwells: Oxford).
- ENGELHARDT, W. 1970. Gestalt und Lebensweise der Ameisenspinne *Synageles venator* (Lucas). *Zugleich ein Beitrag zur Ameisenmimikryforschung*. *Zoologischer Anzeiger* 185: 317-334.
- EVANS, T.A. & MAIN, B.Y. 1993. Attraction between social crab spiders: silk pheromones in *Diaea socialis*. *Behavioral Ecology* 4: 99-105.
- EXLINE, H. & LEVI, H.W. 1962. American spiders of the genus *Argyrodes* (Araneae, Theridiidae). *Bulletin of the Museum of Comparative Zoology* 127: 75-204.
- GILLESPIE, R.G. & CARACO, T. 1987. Risk sensitive

- foraging strategies of two spider populations. *Ecology* 68: 887-899.
- GRAY, M.R. & ANDERSON, G.J. 1989. A new Australian species of *Argyrodes* Simon (Araneidae: Theridiidae) which preys on its host. *Proceedings of the Linnean Society of New South Wales* 111: 25-30.
- GRISWOLD, C.E. 1985. *Isela okuncana*, a new genus and species of kleptoparasitic spider from southern Africa (Araneae: Mysmenidae). *Annals of the Natal Museum* 27: 207-217.
- GRISWOLD, C.E. & MEIKLE-GRISWOLD, T. 1987. *Archaeodictyna ulova*, new species (Araneae: Dictynidae), a remarkable kleptoparasite of group-living cressid spiders (*Stegodyphus* spp., Araneae: Eresidae). *American Museum Novitates* 2897: 1-11.
- HARKNESS, R.D. 1976. Further observations on the relation between an ant *Cataglyphis bicolor* (F.) (Hym., Formicidae), and a spider, *Zodarium frenatum* (Simon) (Araneae: Zodariidae). *Entomologists Monthly Magazine* 112: 111-121.
- HARVEY, P.H. & PAGEL, M.D. 1992. 'The Comparative Method in Evolutionary Biology'. (Oxford University Press: Oxford).
- HINGSTON, R.W.G. 1927. Field observations on spider mimics. *Proceedings of the Zoological Society, London* 1927: 841-858.
- HÖLDOBLER, B. 1971. *Steatoda fulva* (Theridiidae), a spider that feeds on harvester ants. *Psyche* 77: 202-208.
- HÖLDOBLER, B. & WILSON, E.O. 1991. 'The Ants'. (Harvard University Press: Cambridge). 732pp.
- HORTON, C.C. 1979. Apparent attraction of moths by webs of araneid spiders. *Journal of Arachnology* 7: 8.
- HUMPHREYS, W.F. 1988. The ecology of spiders with special reference to Australia. Pp. 1-22. In: A.D. Austin and N.W. Heather (eds). 'Australian Arachnology'. (Australian Entomological Society Miscellaneous Publication No. 5: Brisbane).
- JACKSON, J.F. & DRUMMOND, B.A., III. 1974. A batesian ant-mimicry complex from the Mountain Pine Ridge of British Honduras, with an example of transformational mimicry. *American Midland Naturalist* 91: 248-251.
- JACKSON, R.R. 1985. The biology of *Simuertha paetula* and *S. thoracica*, web-building jumping spiders (Araneae: Salticidae) from Queensland: co-habitation with social spiders, utilization of silk, predatory behaviour and intra-specific interactions. *Journal of Zoology, London (B)* 1: 175-210.
1986. The biology of ant-like jumping spiders (Araneae, Salticidae): prey and predatory behaviour of *Myrmarachne* with particular attention to *M. lupata* from Queensland. *Zoological Journal of the Linnean Society* 88: 179-190.
1987. The biology of *Olios* spp., huntsman spiders (Araneae, Sparassidae) from Queensland and Sri Lanka: predatory behaviour and cohabitation with social spiders. *Bulletin of the British Arachnological Society* 7: 133-136.
- JACKSON, R.R. & BLEST, A.D. 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae: Salticidae) from Queensland: utilization of webs and predatory versatility. *Journal of Zoology, London* 196: 255-293.
- JACKSON, R.R. & BRASSINGTON, R.J. 1987. The biology of *Pholcus phalangoides* (Araneae, Pholcidae): predatory versatility, araneophagy and aggressive mimicry. *Journal of Zoology, London* 211: 227-238.
- JACKSON, R.R. & HALLAS, S.E.A. 1986. Comparative biology of *Portia africanus*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. schultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. *New Zealand Journal of Zoology* 13: 423-489.
1990. Evolutionary origins of displays used in aggressive mimicry by *Portia*, a web-invading araneophagic jumping spider (Araneae: Salticidae). *New Zealand Journal of Zoology* 17: 7-23.
- JACKSON, R.R. & VAN OLPHEN, A. 1991. Prey-capture techniques and prey preferences of *Corythalia canosa* and *Pystira orbiculata*, ant-eating jumping spiders (Araneae, Salticidae). *Journal of Zoology, London* 223: 577-591.
1992. Prey-capture techniques and prey preferences of *Chryssilla*, *Natta* and *Siler*, ant-eating jumping spiders (Araneae, Salticidae) from Kenya and Sri Lanka. *Journal of Zoology, London* 227: 163-170.
- JACKSON, R.R. & WILCOX, R.S. 1990. Aggressive mimicry, prey-specific predatory behaviour and predator recognition in the predator-prey interactions of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. *Behavioral Ecology and Sociobiology* 26: 111-119.
1993. Evidence of predator-prey co-adaptation of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. *Memoirs of the Queensland Museum* 33: 557-560.
- JARMAN, E.A.R. & JACKSON, R.R. 1986. The biology of *Taieria erebus* (Araneae, Gnaphosidae), an araneophagic spider from New Zealand: silk utilisation and predatory versatility. *New Zealand Journal of Zoology* 13: 521-541.
- LARCHER, S.F. & WISE, D.H. 1985. Experimental studies of the interaction between a web-invading spider and two host species. *Journal of Arachnology* 13: 43-59.
- LOPEZ, A. 1987. Glandular aspects of sexual biology. Pp. 121-132. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).
- LUBIN, Y.D. 1974. Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae:

- Araneidae). *Zoological Journal of the Linnean Society* 54: 321-339.
1986. Web building and prey capture in the Uloboridae. Pp. 132-171. In: W. Shear (ed.). 'Spiders: Webs, Behavior and Evolution'. (Stanford University Press: Stanford.)
- MACKAY, W.P. 1982. The effect of predation of Western widow spiders (Araneae: Theridiidae) on harvester ants (Hymenoptera: Formicidae). *Oecologia* (Berlin) 53: 406-411.
- MAIN, B.Y. 1976. 'Australian Spiders'. (Collins: Sydney).
- MATHEW, A.P. 1954. Observations on the habits of two spider mimics of the red ant, *Oecophylla smaragdina* (Fabr.). *Journal of the Bombay Natural History Society* 52: 249-263.
- MCIVER, J. 1987. On the myrmecomorph *Coquillettia insignis* Uhler (Hemiptera: Miridae): arthropod predators as operators in an ant-mimetic system. *Zoological Journal of the Linnean Society* 90: 133-144.
- MCKEOWN, K.C. 1952. 'Australian Spiders: their lives and habits'. (Angus and Robertson: Sydney).
- MILINSKI, M. & PARKER, G.A. 1991. Competition for resources. Pp. 137-168. In: Krebs, J.R. and Davies, N.B. (eds). 'Behavioural Ecology: an evolutionary approach'. (Blackwells: Oxford).
- MYERS, J.G. & SALT, G. 1926. The phenomenon of myrmecoidy, with new examples from Cuba. *Transactions of the Entomological Society of London* 1926: 427-435.
- NENTWIG, W. 1987. The prey of spiders. Pp. 249-263. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).
- NENTWIG, W. & HEIMER, S. 1987. Ecological aspects of spider webs. Pp. 211-225. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).
- NOONAN, G.R. 1982. Notes on interactions between the spider *Eilica pino* (Gnaphosidae) and the ant *Camponotus inca* in the Peruvian Andes. *Biotropica* 14: 145-148.
- OLIVEIRA, P.S. 1988. Ant-mimicry in some Brazilian salticid and clubionid spiders (Araneae: Salticidae, Clubionidae). *Biological Journal of the Linnean Society* 33: 1-15.
- OLIVEIRA, P.S. & SAZIMA, I. 1984. The adaptive bases of ant-mimicry in a Neotropical aphantochilid spider (Araneae: Aphantochilidae). *Biological Journal of the Linnean Society* 22: 145-155.
- PASTEUR, G. 1982. A classificatory review of mimicry systems. *Annual Review of Ecology and Systematics* 13: 169-199.
- POLLARD, S.D., MACNAB, A.M. & JACKSON, J.J. 1987. Communication with chemicals: pheromones and spiders. Pp. 133-141. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).
- PORTER, S.D. 1985. *Masonius* spider: a miniature predator of collembola in harvester-ant colonies. *Psyche* 92: 145-151.
- PORTER, S.D. & EASTMOND, D.A. 1982. *Euryapis coki* (Theridiidae), a spider that preys on *Pogonomyrmex* ants. *Journal of Arachnology* 10: 275-277.
- REICHERT, S. E. 1982. Spider interaction strategies: communication vs. coercion. Pp. 281-315. In: P.N. Witt and J.S. Rovner (eds). 'Spider Communication: Mechanisms and Ecological Significance'. (Princeton University Press: Princeton).
- REICHERT, S.E. & GILLESPIE, R.G. 1986. Habitat choice and utilization in web-building spiders. Pp. 23-48. In: W. Shear (ed.). 'Spiders: Webs, Behavior and Evolution'. (Stanford University Press: Stanford).
- REICHERT, S.E. & LUCZAK, J. 1982. Spider foraging: behavioral responses to prey. Pp. 353-385. In: P.N. Witt and J.S. Rovner (eds). 'Spider Communication: Mechanisms and Ecological Significance'. (Princeton University Press: Princeton).
- REISKIND, J. 1970. Multiple mimetic forms in an ant-mimicking clubionid spider. *Science* 169: 587-588.
1977. Ant-mimicry in Panamanian clubionid and salticid spiders (Araneae: Clubionidae, Salticidae). *Biotropica* 9: 1-8.
- REISKIND, J. & LEVI, H.W. 1967. *Anatea*, an ant-mimicking theridiid spider from New Caledonia (Araneae: Theridiidae). *Psyche* 74: 20-23.
- ROBINSON, M.H. & ROBINSON, B. 1971. The predatory behavior of the ogre-faced spider *Dinopis longipes* F. Cambridge (Araneae: Dinopidae). *American Midland Naturalist* 85: 85-96.
1973. Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smithsonian Contributions to Zoology* 149: 1-76.
1982. Courtship and mating behavior in spiders. *Annual Review of Entomology* 27: 1-20.
- RYPSTRA, A.L. 1981. The effects of kleptoparasitism on prey consumption and web relocation in a Peruvian population of the spider *Nephila clavipes*. *Oikos* 37: 179-182.
- SCHLINGER, E.J. 1987. The biology of Acroceridae (Diptera): true endoparasitoids of spiders. Pp. 319-327. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).
- SHEPARD, M. & GIBSON, F. 1972. Spider-ant symbiosis: *Cotinus* spp. (Araneidae: Salticidae) and *Tapinoma melanocephalum* (Hymenoptera: Formicidae). *Canadian Entomologist* 104: 1951-1954.
- SHINKAI, A. 1988. A note on the web silk theft by *Argyrodes cylindratus* (Thorell) (Araneae: Theridiidae). *Acta Arachnologica* 36: 115-119.
- SMITH, D.D. & DOUGLAS, A.E. 1987. 'The Biology of Symbiosis' (Edward Arnold: London).

- SMITH TRAIL, D. 1980. Predation by *Argyrodes* (Theridiidae) on solitary and communal spiders. *Psyche* 87: 349-355.
- STOWE, M. K. 1986. Prey specialization in the Arancidae. Pp. 101-131. In: W. Shear (ed.). 'Spiders: Webs, Behavior and Evolution'. (Stanford University Press: Stanford).
1988. Chemical mimicry. Pp. 513-587. In: K.C. Spencer (ed.). 'Chemical Mediation of Coevolution'. (Academic Press: New York).
- STOWE, M.K., TUMLINSON, J.H. & HEATH, R.R. 1987. Chemical mimicry: bolas spiders which attract male moth prey emit components of prey sex pheromone blends. *Science* 236: 964-967.
- STRUHSAKER, T.T. 1969. Notes on the spiders *Uloborus mundior* (Chamberlin and Ivie) and *Nephila clavipes* (Linnaeus) in Panama. *American Midland Naturalist* 82: 61-63.
- SUTER, R.B., SHANE, C.M. & HIRSCHEIMER, A.J. 1989. Spider vs. spider: *Frontinella pyramitela* detects *Argyrodes trigonum* via euticular chemicals. *Journal of Arachnology* 17: 237-241.
- TANAKA, K. 1984. Rate of predation by a kleptoparasitic spider, *Argyrodes fissifrons*, upon a large host spider, *Agelena limbatata*. *Journal of Arachnology* 12: 363-367.
- TIETJEN, W.J., AYYAGARI, L.R. & UETZ, G.W. 1987. Symbiosis between social spiders and yeast: their role in prey attraction. *Psyche* 94: 151-158.
- TOFT, C.A., AESCHLIMANN, A. & BOLIS, L. 1991. 'Parasite-Host Associations: Coexistence or Conflict?' (Oxford University Press: Oxford).
- UETZ, G.W. 1988. Group foraging in colonial web-building spiders: evidence for risk sensitivity. *Behavioral Ecology and Sociobiology* 22: 265-270.
1992. Foraging strategies of spiders. *Trends in Ecology and Evolution* 7: 155-159.
- VOLLRATH, F. 1978. A close relationship between two spiders: *Curimagua bayano* synecious on a *Diptera* species. *Psyche* 85: 347-353.
- 1979a. Behaviour of the kleptoparasitic spider *Argyrodes elevatus* (Araneae, Theridiidae). *Animal Behaviour* 27: 515-521.
- 1979b. Vibrations: their signal function for a spider kleptoparasite. *Science* 205: 1149-1151.
1981. Energetic considerations of a spider parasite-spider host system. *Revue Arachnologique* 3: 37-44.
1982. Colony foundation in a social spider. *Zeitschrift für Tierpsychologie* 60: 313-324.
1984. Kleptobiotic interactions in invertebrates. Pp. 61-94 In: C.J. Barnard (ed.). 'Producers and Scroungers: Strategies of Exploitation and Parasitism'. (Chapman and Hall: Beckenham).
- 1987a. Growth, foraging and reproductive success. Pp. 357-370. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).
- 1987b. Kleptobiosis in spiders. Pp. 274-286. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).
- VOLLRATH, F. & PARKER, G.A. 1992. Sexual dimorphism and distorted sex ratios in spiders. *Nature* 360: 156-159.
- WHITEHOUSE, M.E.A. 1986. The foraging behaviours of *Argyrodes antipodiana* (Theridiidae), a kleptoparasite spider from New Zealand. *New Zealand Journal of Zoology* 13: 151-168.
1987. "Spider cat spider": the predatory behaviour of *Rhomphaea* sp. from New Zealand. *Journal of Arachnology* 15: 355-362.
- 1988a. Factors influencing specificity and choice of host in *Argyrodes antipodiana* (Araneae, Theridiidae). *Journal of Arachnology* 16: 349-355.
- 1988b. To mate or fight? Male-male competition and alternative mating strategies in *Argyrodes antipodiana* (Theridiidae, Araneae). *Behavioural Process* 23: 163-172.
- WING, K. 1983. *Tutelina similis* (Araneae: Salticidae): an ant mimic that feeds on ants. *Journal of the Kansas Entomological Society* 56: 55-58.
- WISE, D.H. 1982. Predation by a commensal spider, *Argyrodes trigonum*, upon its host: an experimental study. *Journal of Arachnology* 10: 111-116.
- YEARGAN, K.V. 1988. Ecology of a bolas spider, *Mastophora hutchinsoni*: phenology, hunting tactics, and evidence for aggressive chemical mimicry. *Oecologia* 74: 524-530.